A REVIEW OF RECENT STUDIES OF SOUTHERN OCEAN LIPARIDAE (TELEOSTEI: SCORPAENIFORMES)

by

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ABSTRACT. - At present about 90 species of 7 genera of Liparidae fishes are discovered and described from the Southern Ocean and adjacent waters. Reducing trend in the morphological transformation of the pectoral girdle during evolution of *Careproctus* and *Paraliparis* in depths of the Southern Ocean is traced. Bathymetric analysis shows that species of *Careproctus* are distributed in the Antarctic in much deeper water than *Paraliparis*. The problem of origin and depth distribution of the southern Liparidae is discussed.

RÉSUMÉ. - Revue des études récentes sur les Liparidae de l'Océan Austral (Teleostei: Scorpaeniformes).

À ce jour, environ 90 espèces de Liparidae, réparties en 7 genres, ont été découvertes et décrites de l'Océan Austral et des mers adjacentes. La réduction, au cours de l'évolution, de la ceinture pectorale chez les espèces de profondeur des genres *Careprotus* et *Paraliparis* de l'Océan Austral, est décrite. L'analyse des répartitions bathymétriques montre que les espèces du genre *Careprotus* se situent plus profondément dans les eaux antarctiques que les espèces du genre *Paraliparis*. Le problème de l'origine et de la distribution bathymétrique des Liparidae de l'Océan Austral est discuté.

Key-words. - Liparidae, PSE, PSW, Antarctic, Southern Ocean, Pectoral girdle, Depth distribution.

The fish fauna of the Antarctic is usually characterized as the kingdom of notatheniiform fishes. But new investigations have greatly changed the situation since the number of discovered species, having the past North Pacific origin has considerably increased. These are mainly numerous species of liparid (60 species), zoarcid (29) fishes and also 3 species of the so-called soft sculpins (Cottunculidae) and may be some species of *Bathyraja* (Stehmann, 1986; Andriashev, 1987, 1991).

For about 20 years, I have been given much time to study the morphology and systematics of the Liparidae, especially from the Antarctic. This group of fishes is notable by a great morphology and species diversity and, as is known, is difficult for taxonomists. Liparidae are widely distributed in cold and temperate waters of all oceans from intertidal zone to depths of 7,587 m. But only few poorly studied liparid species were known not long ago in great region of the southern hemisphere. Our knowledge on the problem given however has sufficiently changed during the last 10 or 15 years. For example, the recent monograph "Fishes of the Southern Ocean" (Gon and Heemstra, 1990) includes the only species of the genus *Careproctus*. But now 41 southern species of this genus are known. At present about 90 species and 7 genera of the liparids are discovered and described from the south hemisphere (Stein and Tompkins, 1989; Andriashev and

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Prirodina, 1990; Duhamel, 1992; Andriashev, 1992b, 1994; Andriashev and Stein, 1998). The greatest part of the species belongs to two large genera, *Careproctus* and *Paraliparis*, other genera include only single or few species (Table I, Fig. 1). All new species of *Paraliparis* are published (Andriashev, 1986, 1994; Stein and Tompkins, 1989; Stein *et al.*, 1991; Duhamel, 1992) but 18 new Antarctic species of *Careproctus* have been recently described (Andriashev and Stein, 1998). Thus, at present the diversity of the liparid fish fauna of the southern hemisphere is quite comparable with the liparid species native from area North Pacific and is several times more than in both, the Arctic (10) and North Atlantic (16 species, pers. data).

Liparid fishes are a specialized branch of the cottoid stem of scorpaeniform fishes. Their ventral fins are transformed into a sucking disk which is of adaptive significance, especially for inshore species. During the evolution of liparids in the environment of deep-sea and midwater considerable morphological transformations occurred which are mostly of reducing trend. One can judge it because most part of apomorphic features are connected with their simplification, reduction and atrophy. Thus the sucking disk became smaller and completely disappeared; the trilobed multiserial teeth simplified to one row of conic teeth and atrophied; pleural ribs shortened and lost; bones of urostyle complex fused together or atrophied; the number of rays in pectoral fin reduced from 40 to 12, in caudal fin from 14 to 4 rays. But morphological transformations of shoulder girdle are especially significant; its morphology was studied in 83 species of all genera of the southern liparids.

REDUCTION OF PECTORAL RADIALS

The most plesiomorph condition of pectoral girdle is common for species of the genus *Liparis* from the north hemisphere (Fig. 2): deep notches in pectoral radials, radial formula R(3+1) and three interradial fenestrae in the basal cartilaginous lamina of the shoulder girdle; also two pairs of strong pleural ribs and two separate hypural plates. These are distinctly plesiomorph features for the family Liparidae. Quite similar to *Liparis* is the morphology of the pectoral girdle of one of the most generalized antarctic species of the genus *Careproctus*, *C. parini* Andriashev & Prirodina (Fig. 3A). It is characterized by the presence of the following plesiomorph characters: 4 radials with 5 notches, radial formula R(3+1); teeth trilobed, sharp; two pairs of strong pleural ribs present; hypural plate well divided; high number of rays in pectoral fin (38) and numerous caudal rays (14).

Table I. - The number of the southern liparid fishes.

Genera	Antarctic Ocean	The southern hemisphere
Notoliparis Andriashev	2	3
Careproctus Kröyer	27	41
Eknomoliparis Stein	1	1
Genioliparis Andriashev & Neelov	1	1
Paraliparis Collett	32	42
Edentoliparis Andriashev	1	1
Psednos Barnard	?	1
Total	64	90

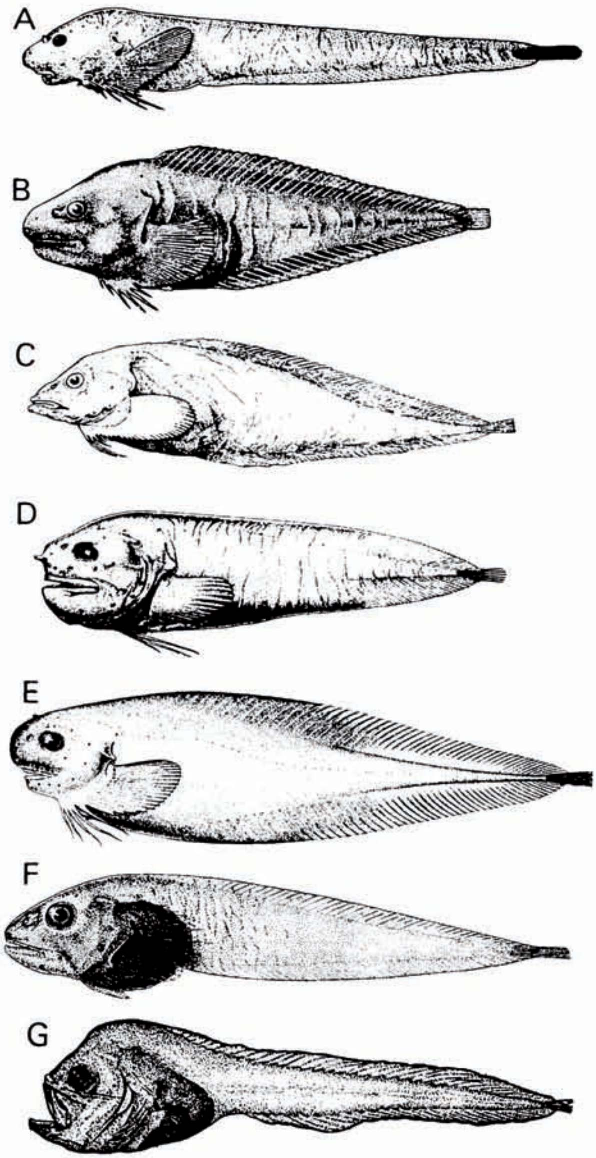

Fig. 1. - Species of 7 liparid fish genera of the southern hemisphere: A: *Notoliparis macquariensis*. B: *Careproctus parini*. C: *Eknomoliparis chirichignoi*. D: *Genioliparis lindbergi*. E: *Paraliparis valentinae*. F: *Edentoliparis terraenovae*. G: *Psednos micrurus*.

A similar pectoral girdle also exists in an antarctic species, *C. catherinae* Andriashev & Stein, and in only four more northern species (Table II), while nearly all species of *Care-*

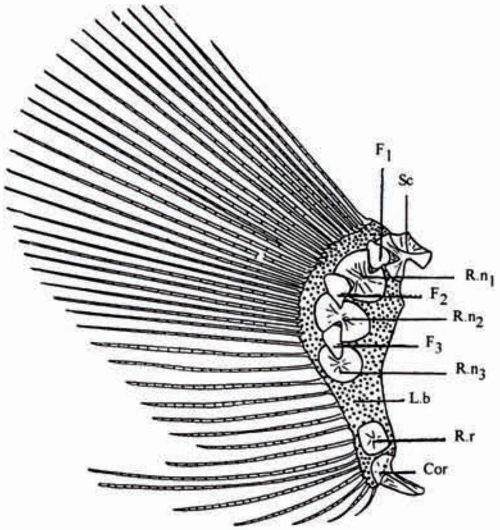

Fig. 2. - Pectoral girdle of the genus *Liparis*. Cor: coracoid. F1-3: fenestrae. L.b.: basal cartilaginous lamina. R.n1-3: notched radials. R.r.: round radial. Sc: scapula.

proctus in North Pacific are of primitive type, having notched radials, interradial fenestrae, strong pleural ribs, etc. (Pitruk, 1991).

All the other 35 southern species of *Careproctus* have only round pectoral radials without notches and interradial fenestrae. During the process of specialization the number of pectoral radials in species of *Careproctus* decreased (to 3 and 2), pleural ribs become shortened and lost, hypural plates are grown together, the number of pectoral and caudal rays decreased, etc. So, *C. aureomarginatus* Andriashev has 4 round radials (radial formula R(3+1), Fig. 3B), the lowest of which is spaced from the third radial by a wider interspace (as in *Liparis*). Such comparatively primitive arrangement is also found in 3 other southern species (see Table II). *C. georgianus* Lönnberg also has 4 round radials but they are arranged equidistantly (radial formula R(1+1+1+1), Fig. 3C). This a bit more derived arrangement is common for a large group of the Patagonian and Antarctic species (Table II).

The number of radials is decreased to 3 (radial formula R(2+0+1), Fig. 3D) in *C. continentalis* Andriashev & Prirodina and in 8 other Patagonian and Antarctic species (Table II). And finally, the number of radials is reduced to 2 (radial formula R(1+0+0+1), Fig. 3E) in *C. acifer* Andriashev & Stein and in a large group of mainly antarctic bathyal-abyssal living species (Table II). One may suppose that two antarctic species (*C. longepectoralis* Duhamel and *C. profundicola* Duhamel) also may belong to this group.

Similar process of reduction takes place independently in the genus *Paraliparis*, all numerous species of which lost their sucking disk and pleural ribs. Therefore, the process of reduction began at a more derived stage than in *Careproctus*. The most primitive species of *Paraliparis* is *P. stehmanni* Andriashev because it is the only species of the genus with well notched radials (radial formula R(3+1) and the presence of interradial fenestrae (Fig. 4A).

A number of mainly antarctic species also has 4 radials (radial formula R(3+1), Fig. 4B) but they are round (Table III). This group of species of *Paraliparis* (Table III) is

Table II. - List of the southern species of *Careproctus* with data on their distribution and pectoral radial formula (N: notched; R: round radials).

Species	Distribution	Depth in m	Pectoral radial formula
C. albescens Barnard	S. Africa.	600-1460	N(3 + 1)
C. herwigi Andriashev	N. Argentina	1250	N(3 + 1)
C. novaezelandiae Andriashev	SE New Zealand slope	954-971	N(3 + 1)
C. parini Andriashev & Prirodina	S. Shetland Is	750-1116	N(3 + 1)
C. smirnovi Andriashev	S. Argentina	1500-1570	N(3 + 1)
C. aureomarginatus Andriashev	S. off Falkland Is	1660-1665	R(3 + 1)
C. credispinulosus Andriashev & Prirodina	S. Georgia Id	769-1400	R(3 + 1)
C. inflexidens Andriashev & Stein	Ross Sea	2049-2089	R(3 + 1)
C. pallidus Vaillant	Tierra del Fuego	6-28	R(3 + 1)
C. atrans Andriashev	Northward of Falkland Is.	1300	R(1+1+1+1)
C. cactiformis Andriashev	S. Argentina	399-536	R(1+1+1+1)
C. falklandicus (Lönnberg)	Falklands-Burdwood area	16-150	R(1+1+1+1)
C. georgianus Lönnberg	S. Georgia Id	85-285	R(1+1+1+1)
C. macranchus Andriashev	N. Argentina	1550-1600	R(1+1+1+1)
C. sandwichensis Andriashev & Stein	S. Sandwich Trench	5435-5459	R(1+1+1+1)
C. scaphopterus Andriashev & Stein	Scotia Sea	2886-3623	R(1+1+1+1)
C. steini Andriashev & Prirodina	S. Shetland Is	429-583	R(1+1+1+1)
C. tricapitidens Andriashev & Stein	Brandsfield Str.	662-1120	R(1+1+1+1)
C. zispi Andriashev & Stein	Scotia Sea	1922-2229	R(1+1+1+1)
C. acaecus Andriashev	S. Argentina	750	R(2+0+1)
C. aculeolatus Andriashev	N off Falkland Is	540-700	R(2+0+1)
C. armatus Andriashev	S off Falkland Is	1210-1290	R(2+0+1)
C. improvisus Andriashev & Stein	S. Georgia Id	260-306	R(2+0+1)
C. lacmi Andriashev & Stein	Scotia Sea	3817-3931	R(2+0+1)
C. parviporatus Andriashev & Stein	Scotia Sea	3817-3931	R(2+0+1)
C. polarsterni Duhamel	NE Weddell Sea	425-830	R(2+0+1)
C. sp. Andriashev	Guevara Bank,Scotia Sea	952	R(2+0+1)
C. acifer Andriashev & Stein	Scotia Sea	2906-2946	R(1+0+0+1)
C. atacamensis Andriashev	Atakama Trench	3070-2710	R(1+0+0+1)
C. eltanini Andriashev & Stein	Scotia Sea	2869-3038	R(1+0+0+1)
C. fedorovi Andriashev & Stein	Scotia Sea	3817-3931	R(1+0+0+1)
C. leptorhinus Andriashev & Stein	Scotia Sea	4246-4295	R(1+0+0+1)
C. minimus Andriashev & Stein	Budrwood Bank	124-128	R(1+0+0+1)
C. pseudoprofundicola Andriashev & Stein	Ross Sea	2049-2089	R(1+0+0+1)
C. rimiventris Andriashev & Stein	Scotia Sea	1976-2068	R(1+0+0+1)
C. vladibeckeri Andriashev & Stein	S.Weddell and Ross seas	2273-2941	R(1+0+0+1)
C. longepectoralis Duhamel	NE Weddell Sea	2025-2027	R?(1+0+0+1)
C. profundicola Duhamel	Banzare Banks	1820-2000	R?(1+0+0+1)

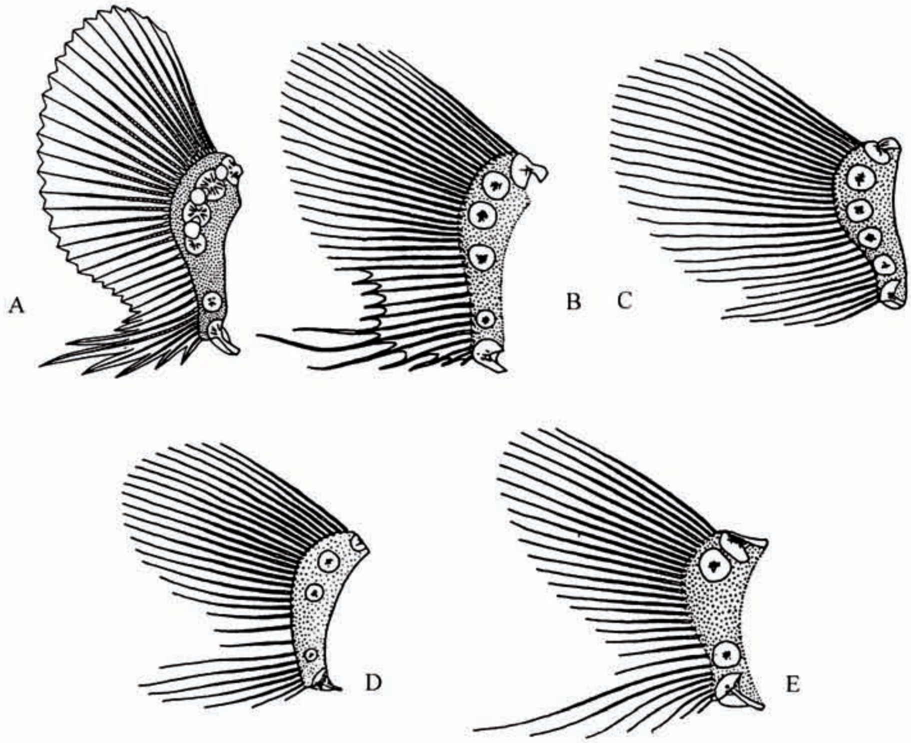

Fig. 3. - Pectoral girdle of *Careproctus* spp. A: *C. parini*. B: *C. aureomarginatus*. C: *C. georgianus*. D: *C. continentalis*. E: *C. acifer*.

characterized by the presence of 4 but equidistantly arranged radials (radial formula R(1+1+1+1)) as well as in *P. hubbsi* Andriashev (Fig. 4C).

The number of radials is decreased to 3 (radial formula R(2+0+1)) in *P. monoporus* Andriashev & Neelov (Fig. 4D) and also in other six Patagonian and Antarctic species (Table III). And finally, the number of radials is reduced to 2 radials (radial formula R(2+0+0)) dorsally arranged radials as in *P. trunovi* Andriashev (Fig. 4E) and in some other mainly south Atlantic species (Table III).

The arrangement of two last pectoral radials is of importance for understanding the phylogeny of the southern liparids. The evolutionary process of the radial reduction is schematized on figure 5. The process of reduction is going on in parallels in genera *Careproctus* and *Paraliparis* and it is similar in both genera up to the stage of three radials. The subsequent process of reduction is different in these genera: all two-radial species of *Careproctus* studied (12 species) have two opposed radials remained, radial formula R(1+0+0+1), one below scapula and second above coracoid. On the contrary, all known two-radial species of *Paraliparis* (9 species) have always dorsally arranged radials, both below scapula, radial formula R(2+0+0). This difference in the ways of the radial reduction confirms the presence of two main different phyletic branches in the evolution of the southern liparids (Fig. 5).

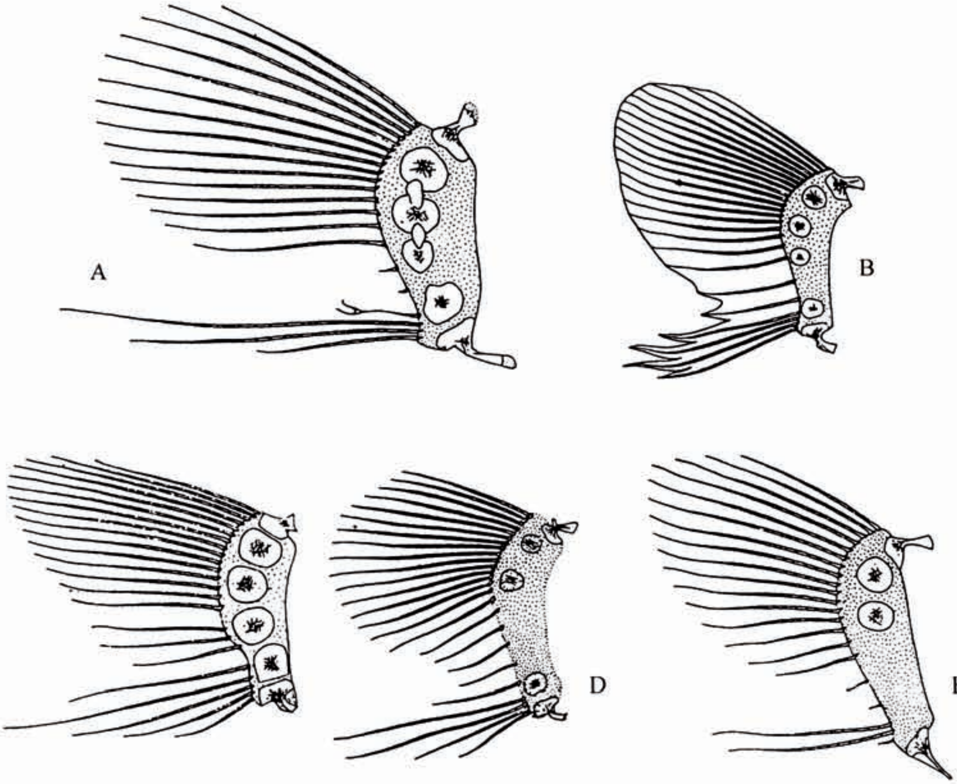

Fig. 4. - Pectoral girdle of *Paraliparis* spp. A: *P. stehmanni*. B: *P. leucogaster*. C: *P. hubbsi*. D: *P. monoporus*. E: *P. trunovi*.

SOME OTHER ENDEMIC SOUTHERN LIPARIDS

The endemic southern genus *Notoliparis* is of special interest among the southern liparids by the plesiomorph condition of its cephalic seismosensorial pores. All species of the genus have retained the ancestral (cottoid) arrangement of pores in supraorbital and temporal canals: one coronal pore, one pair of postcoronal pores and 4 pairs of pores in temporal canals. Pectoral radial formula in two species is R(1+1+1+1). This genus consists of three valid species known only from deep trenches: *N. kurchatovi* Andriashev from the South Orkney Trench at a depth of 5474-5465 m, *N. macquariensis* Andriashev (Fig. 1A) from the Macquarie Hjort Trench (5400-5410 m) and *N. kermadecensis* (Nielsen) from the Kermadec Trench (6660-6770 m). Ocean trenches deeper than 6 kilometres are named ultra-abyssal zone by Russian marine biologists (Belyaev, 1972), but the term hadal proposed by Bruun (1956) is more often used. The matter is not in the terms but in difference in the species composition of the hadal fauna compared to the surrounding abyssal faunas as was grounded by Birstein (1957) and Belyaev (1972).

Table III. - List of the southern species of *Paraliparis* with new data on their distribution and pectoral radial formula (N: notched; R: round radials).

Species	Distribution	Depth in m	Pectoral radial formula
P. stehmanni Andriashev	Scotia Sea	2600	N(3 + 1)
P. copei gibbericeps Andriashev	S. Georgia	400-1000	R(3 + 1)
P. copei kerguelensis Andriashev	Kerguelen and Crozet	510-1050	R(3 + 1)
P. copei wilsoni Richards	S. Africa	885-1830	R(3 + 1)
P. fuscolingua Stein et Tompkins	Ross Sea	2273	R(3 + 1)
P. leucogaster Andriashev	Bransfield Str.	210-260	R(3 + 1)
P. leucoglossus Andriashev	Lazarev Sea, East Antarctica	900-960	R(3 + 1)
P. mawsoni Andriashev	East Antarctica	735-1020	R(3 + 1)
P. meganchus Andriashev	S.Shetland, S. Orkney Id	220-850	R(3 + 1)
P. trilobodon Andriashev & Neelov	S. Shetland	315-335	R(3 + 1)
P. andriashevi Stein & Tompkins	Ross Sea	1883-1890	R(1+1+1+1)
P. antarcticus Regan	East Antarctica	300-782	R(1+1+1+1)
P. diploprora Anadriashev	Scotia Sea off S. Georgia	2600	R(1+1+1+1)
P. eltanini Stein & Tompkins	Magellan Str.	485	R(1+1+1+1)
P. gracilis Norman	S. Georgia and Crozet Is	217-1055	R(1+1+1+1)
P. hubbsi Andriashev	Northern Argentina	1300-1560	R(1+1+1+1)
P. leobergi Andriashev	East Antarctica	165-450	R(1+1+1+1)
P. molinai Stein, Melendez & Kong	Chile	800	R(1+1+1+1)
P. operculosus Andriashev	Kerguelen	380-1010	R(1+1+1+1)
P. somovi Andriashev & Neelov	S. Shetland	406-850	R(1+1+1+1)
P. valentinae Andriashev & Neelov	Cosmonaut and Weddell seas	800-1100	R(1+1+1+1)
P. anarthractae Stein & Tompkins	Magellan Str.	3-55	R(2+0+1)
P. aspersus Andriashev	Argentina	800-846	R(2+0+1)
P. debueni Abdriashev	Chile	440-470	R(2+0+1)
P. devriesi Andriashev	Ross Sea	500-800	R(2+0+1)
P. incognita Stein & Tompkins	East Antarctica	500-800	R(2+0+1)
P. neelovi Andriashev	Banzare Banks	1070-2000	R(2+0+1)
P. australis Gilchrist	S. Africa	295-571	R(2+0+0)
P. cerasinus Andriashev	Risser Larsen Sea	950-1100	R(2+0+0)
P. duhameli Andriashev	Crozet Id	955-1055	R(2+0+0)
P. kreffti Andriashev	Scotia Sea	850-2600	R(2+0+0)
P. tetrapteryx Andriashev & Neelov	S. Georgia	500-830	R(2+0+0)
P. thalassobathyalis Andriashev	Banzare Banks	1160-1600	R(2+0+0)
P. thalassobathyalis subsp. Andriashev	Meteor Seamount	960-1100	R(2+0+0)
	Shag Rocks, S. Georgia Id	620-635	R(2+0+0)
P. trunovi Andriashev	Meteor Seamount	960-1010	R(2+0+0)

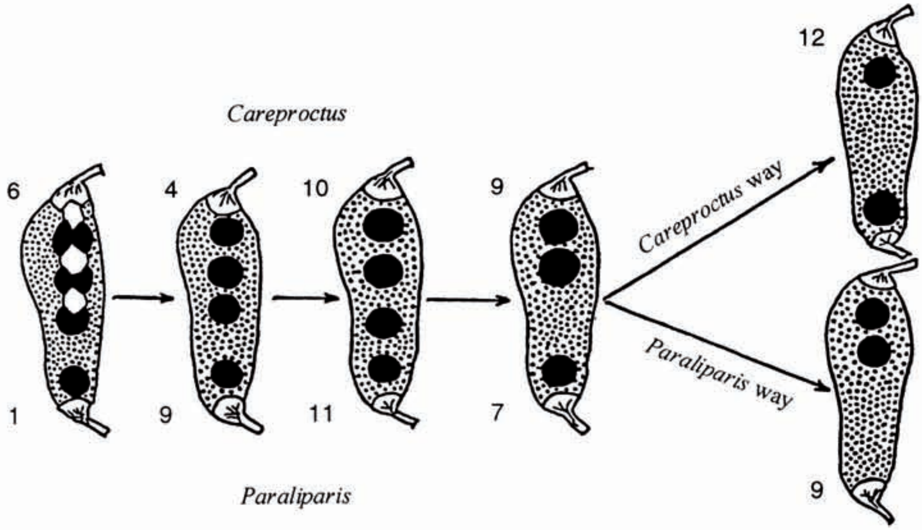

Fig. 5. - Scheme of reduction of the pectoral radials in the southern species of *Careproctus* and *Paraliparis*. The numbers indicate the number of species in genera *Careproctus* and *Paraliparis*.

Rather peculiar liparid fish with a sucker disk, *Eknomoliparis chirichignoae* Stein, Meléndez & Kong (Fig. 1C) was described from the tropical waters along northern Chile (Stein *et al.*, 1991); it has unusual arrangement of nasal bones, a wedge-form head, specialized tail vertebrae and pectoral radial formula R(3+1).

The largest of southern liparids is *Genioliparis lindbergi* Andriashev & Neelov (1976) reaching TL of 31 cm. It is distinguished by a massive mandible and the presence of four barbellike appendixes around its wide snout; ventral disk is absent but pectoral radials are notched, with interradial fenestrae. *G. lindbergi* is known only from the South Shetland Islands (735-830 m) and is similar in some respects to the northern liparid fish, *Odontoliparis ferox* Stein (1978) from off Oregon (2884 m).

It is worthy to note the genus *Psednos*, species of which I named the dwarf snailfishes. Species of *Psednos* are notable for their unusual morphology of the cephalic seismosensorial canals, a small size of mature specimens (35-40 mm), pectoral radial formula R(1+1+1), purely pelagic mode of life and bipolar (exactly antitropical) pattern of distribution. Generic validity of *Psednos* has been reestablished only recently (Andriashev, 1992a). This group of liparid fishes is scarcely studied, but besides the South African *Psednos micrurus* Barnard (Fig. 1G) and the North Atlantic *P. christinae* Andriashev, several undescribed representatives of the genus were found out in the Tasman Sea, south of Australia and New Zealand and in the north hemisphere off California and in the Gulf of California (David L. Stein, pers. comm.).

Another derived liparid fish is *Edentoliparis terraenovae* (Regan) (Fig. 1F). This high-Antarctic endemic is notable for its purely pelagic mode of life and the total absence of teeth in both the jaw and the pharyngeal apparatus.

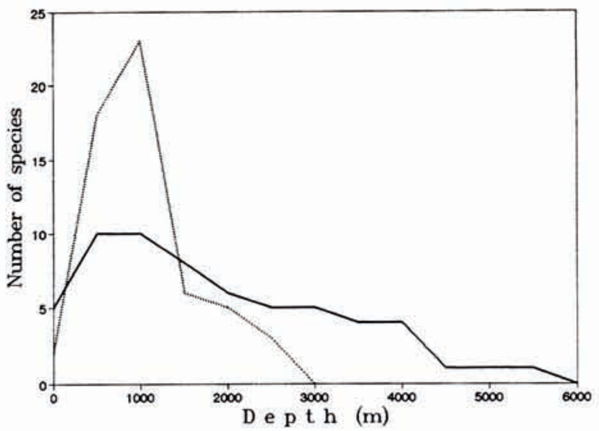

Fig. 6. - Bathymetric distribution of *Careproctus* (41 species; solid line) and *Paraliparis* (42 species; dotted line) in the southern hemisphere.

GEOGRAPHICAL AND BATHYMETRIC DISTRIBUTION

Geographical distribution of liparid fishes in the Southern Ocean is not enough studied up to now as most part of species was described from a single or a few specimens. But recently the validity of many my newly described species of *Paraliparis* has been confirmed by Stein and Tompkins (1989) and Duhamel (1992). Nevertheless, our data on the distribution of southern liparid species are fragmentary and therefore are insufficient for zoogeographic subdivision of the south hemisphere waters. We can only conclude that the species composition is quite different in such vast areas as the Antarctic deep shelf, Subantarctic Islands, Patagonia-Falkland area, South Africa and New Zealand bathyal zones, abyssal depths of the Antarctic.

The result of bathymetric analysis turned out to be quite unexpected as many species of *Careproctus* were found on greater depths than species of *Paraliparis* (Fig. 6). Species of *Careproctus* inhabit wide depth range from intertidal zone to 5500 m and are usual at great abyssal depths. Fifteen southern species of *Careproctus* were discovered at depths of about 2000 m or deeper, from which 9 species are known at depths about 3000-4000 m and one species was found at 5459 m. In the southern hemisphere the species of *Paraliparis* have not been discovered at depths of about 3000 m and only 6 species found up to 2000 m or a little deeper. The other 36 species of *Paraliparis* are distributed in a rather narrow range of the shelf and upper bathyal depths (200-1500 m). It is notable that 6 species of *Paraliparis* inhabit the Antarctic Continent shelf (165-420 m) and 8 species are found on the shelf of South Georgia and subantarctic islands. On the contrary, the few shallow species of *Careproctus* inhabit only temperate waters; species of *Careproctus* are rare on the Antarctic shelf (2 species in the Weddell Sea and 2 species at South Georgia). A quite different picture is observed in the northern hemisphere, as species of *Paraliparis* always inhabit in much deeper waters than *Careproctus* there. The cause of such reserve depth distribution is unclear for the present but one may suppose that it is connected with different geologic times of the penetration of species of *Careproctus* and *Paraliparis* into the Southern Ocean.

CONCLUSION

Some words about the origin of Liparidae in the Southern Ocean. Fundamental works by Peter Schmidt (1904) and Burke (1930) stated that the native area of liparids is the North Pacific. Then Regan (1914) proposed an idea about the penetration of zoarcid species by bathyal depths along the Pacific side of America to the Tierra del Fuego. This has been confirmed by my data and also developed for the family Liparidae (Andriashev, 1986). In that area both families made up their secondarily center of speciation in bathyal zone and at shelf. This is a rare example of the formation of shelf and even true intertidal fauna from deep-sea migrants (Andriashev, 1965).

After the spreading of the Drake Passage (about 20-22 million years ago; Barker and Barrel, 1977) southern liparids received a possibility to penetrate into the South Atlantic. The probability of such kind of long pathway has been grounded in details in my hypothesis of transoceanic (non-arctic) dispersal of secondarily deep-sea liparids from the north Pacific around an area of the Drake Passage into the Indian Ocean, the North Atlantic and even into the depths of the Polar basins (Andriashev, 1991).

An unexpected confirmation of my hypothesis of transoceanic dispersal has been recently received. Several liparid specimens trawled by the modern British expeditions aboard "Discovery" at depths about 3000-4000 m near the Porcupine Seabight (eastern North Atlantic off Ireland) have been received kindly from N. Merrett and identified as three new species. All these species are distinctly of the south oceanic origin as they have unique Antarctic features, only two pectoral radials, with radial formula R(1+0+0+1) in *Careproctus* and R(2+0+0) in *Paraliparis*. Thus, it may be noted that the morphological features confirm the biogeographic speculation on transoceanic past pathway of liparid migrants (Andriashev, 1991).

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